

Life-support system of the Prince Edward Archipelago: overview of local and advected resources

by

Leigh J. GURNEY* (1, 2), Evgeny P. PAKHOMOV (1) & Brian P.V. HUNT (1)

ABSTRACT. - A conceptual model called the 'Life Support System' (LSS) exists for the Prince Edward Islands (PEI), which describes the contributions of local and advected production sources to the island system. The aim of this study is to quantify, for the first time, the relative importance of these sources of primary production to the PEIs food web at a range of spatial scales. A set of four nested mass-balanced ecosystem models of decreasing size, centered on the islands were created. Each model consisted of 21 functional groups constructed using fifty years of biological research including recent stable isotope studies to represent the ecosystem in the 1980s. Advected allochthonous resources were found to dominate the system at all but the smallest spatial scale, where autochthonous local resources were important. Macrophytes were found to be the most important local resource, with this production entering the system directly as well as in its detrital form. Island-associated blooms were found to contribute the least to the system. Incorporation of the microbial food web into the model would improve the understanding of the system, which requires further investigation.

RÉSUMÉ. - Système moteur de production marine au large de l'archipel du Prince Edward : part des ressources locales et injectées.

Un modèle conceptuel nommé 'Life Support System' (LSS) est développé pour les îles du Prince Edward (PEI). Il décrit les contributions des sources de production locales et injectées au système péri-insulaire. L'objectif de cette étude est, pour la première fois, de quantifier l'importance relative de ces sources de production primaire contribuant au réseau trophique de PEI dans une gamme d'échelles spatiales. Un jeu de quatre modèles écosystémiques, emboîtés et pondérés en poids, de taille décroissante et centrés sur les îles a été créé. Chaque modèle est constitué de 21 groupes fonctionnels utilisant cinquante années de recherches biologiques incluant les études récentes sur les isotopes stables pour représenter l'écosystème dans les années 1980. Le système est dominé dans son ensemble par les ressources allochtones injectées, mais pour les plus petites échelles spatiales les ressources locales autochtones se sont révélées importantes. Les plus importantes ressources locales sont les Macrophytes, leur production entrant directement dans le système ou sous forme décomposée. Les blooms associés à l'effet d'île contribuent aussi pour partie au système. L'incorporation de la boucle microbienne au modèle améliorerait la compréhension du système ce qui nécessite d'autres recherches.

Key words. - Primary producers - Prince Edward Islands - Ecosystem model - Ecopath.

Oceanic islands are known to have an effect on the surrounding waters resulting in increased productivity. This phenomenon is known as the 'island mass effect' (Doty and Oguri, 1956). The Southern Ocean is, in general, characterised as a high nutrient, low productivity (HNLP) region. However, many sub-Antarctic islands, including the Prince Edward Islands (PEI), are hotspots of biological productivity and are host to millions of seabirds and seals which use the islands as a breeding ground and refuge (Pakhomov and Chown, 2003).

A conceptual model called the 'Life Support System' (LSS) has been created for the PEI to describe how these islands are able to support the high biomass of top predators on the islands (Pakhomov and Froneman, 1999b; Pakhomov and Chown, 2003). The LSS as it stands now has 'offshore' and 'inshore' components that are named after the categories for the source of the supporting production. The 'offshore'

component may be considered the allochthonous, or oceanic input, production that is advected into the system. This open ocean productivity is generally low (Hempel, 1985; Pakhomov and Froneman, 1999b). The 'inshore' component is the autochthonous production of the system and includes both island-associated phytoplankton blooms and near-shore macrophyte production. It is this production that is associated with the 'island mass effect'.

Islands create the 'island mass effect' in a number of ways. It has been demonstrated that in the HNLP Southern Ocean input of iron from islands and their shallow shelves into the surrounding waters increases productivity (Atkinson *et al.*, 2001; Blain *et al.*, 2001; Blain *et al.*, 2008). Islands also create a disturbance in the flow of the incident current resulting in turbulence and mixing which may provide suitable conditions for elevated production associated with the islands, also known as 'island stirring' (Mann and Lazier,

(1) Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, V6T 1Z4, BC, Canada.
[epakhomov@eos.ubc.ca] [bhunt@eos.ubc.ca]

(2) European Commission, Joint Research Centre, Institute for Environment and Sustainability, Ispra, 21027, VA, Italy.

* Corresponding author [leigh.gurney@jrc.ec.europa.eu]

1996). At the neighbouring Crozet archipelago (Atkinson *et al.*, 2001; Bakker *et al.*, 2007) and the Kerguelen plateau (Armand *et al.*, 2008) as well as at the PEI (Perissinotto *et al.*, 2000), observed increases in productivity in the vicinity of, or downstream of the islands have been attributed to the 'island mass effect'. Island shelf regions provide substrate for near-shore macrophyte production, and runoff from the islands may carry nutrients from top predator populations that reside on the islands aiding the benthic production and resulting in surface stratification potentially enhancing local phytoplankton productivity as observed at the PEI (Perissinotto and Duncombe Rae, 1990).

The oceanography around the PEI is complex because of a combination of the frontal features, the bathymetry and the interaction with the islands themselves (Ansorge and Lutjeharms, 2002; 2003; 2005). Two frontal features are found in the vicinity of the islands: the Sub-Antarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south (Deacon, 1983; Lutjeharms, 1985; Nowlin and Klinck, 1986) (Fig. 1). The position of these fronts is dynamic and variable (Lutjeharms and Valentine, 1984; Duncombe Rae, 1989a; Lutjeharms *et al.*, 2002) and their proximity (the SAF in particular) is hypothesised to have a significant effect on the hydrodynamics at the islands. When the SAF is close to the islands, the increased current velocities associated with this front are predicted to lead to a flow-through system between the islands (Pakhomov and Froneman 1999a; Ansorge and Lutjeharms, 2000), and advected sources of primary productivity dominate the system. Conversely, when the SAF is further north, lower velocities of the inter-frontal zone are predicted to result in water retention over the inter-island shelf and as a consequence, little exchange of inshore/offshore waters over the inter island region occurs (Perissinotto and Duncombe Rae, 1990). Cross advection over the PEI shelf when the SAF is

far to the north of the islands has been observed (Hunt *et al.*, 2008). However, there is little doubt that phytoplankton blooms can and do occur in the vicinity of the islands (Allanson *et al.*, 1985; Duncombe Rae, 1989b; Perissinotto and Duncombe Rae, 1990). A number of mechanisms for on-shelf water retention have been postulated in the past, including upwelling (Grindley and David, 1985), eddy formation (Allanson *et al.*, 1985) and Taylor column formation (Perissinotto and Duncombe Rae, 1990); however oceanographic data to support such findings are lacking. More recent studies have found mesoscale eddies up and downstream of the islands (Ansorge and Lutjeharms, 2002; 2003; Ansorge *et al.*, 2004; Durgadoo *et al.*, 2010). Observed elevated phytoplankton production may be the result of the trapping of these eddies over the island shelf, as has been observed at other Southern Ocean islands like South Georgia (Whitehouse *et al.*, 1999). A summary of current knowledge points to the dynamics of frontal systems as the drivers of shelf-water retention, and consequently of the relevant contributions of allochthonous and autochthonous phytoplankton (Perissinotto *et al.*, 2000; Ansorge and Lutjeharms, 2002).

The second form of autochthonous production is composed of benthic macrophytes. Two kelp species dominate the biomass, the endemic *Macrocystis laevis* (Hay, 1986) and *Durvillaea antarctica* (Chamisso) (Hariot, 1892). *Macrocystis laevis* occurs along the lee shore of Marion Island, and is generally found between 5 and 20 m depth (Attwood *et al.*, 1991) but may be found at depths of up to 68 m in areas where the substrate is favourable (Perissinotto and McQuaid, 1992a). *Durvillaea antarctica* occurs in the infralittoral fringe of the islands (Beckley and Branch, 1992).

The aim of this study is to quantify, for the first time, the relative importance of the three sources of primary production to the PEI food web. The relative contribution of each of the three primary production sources will differ depending on the spatial scale at which the system is considered. This will be tested by developing Ecopath models with four different boundary sizes. A preliminary investigation into the ecosystem boundary size, as determined by the centrally placed foragers, found that all energetic requirements for the inhabitants of the PEI could be met at the scale of the Economic Exclusion Zone (EEZ) (Gurney *et al.*, 2008). For this reason, the EEZ (i.e., a circular area of 200 nautical mile (nm) radius centred on the islands), was chosen as the largest model considered, and a series of sequentially smaller models, the smallest of which was chosen to represent the island shelf area (radius of 20 nm) were used. Using the top-down approach of assessing consumer impacts on primary producers and ecosystem mass balance, we aimed to quantitatively evaluate the previous conceptual models of the PEI LSS.

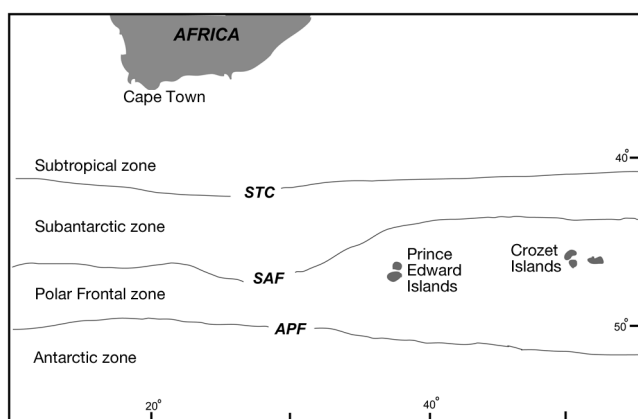


Figure 1. - Map of the Indian sector of the Southern Ocean showing the position of the Prince Edward Islands and main frontal features (STC, Subtropical Convergence; SAF, Sub-Antarctic Front; APF, Antarctic Polar Front).

METHODS

The Ecosystem model

A mass-balanced network model (Ecopath) was used to construct an ecosystem model of the PEI. The basic model is a closed system formulation of the functional groups in an ecosystem and the full methodology can be found in the user's guide (Christensen *et al.*, 2004). Each group (functionally related group or a single species) is represented by their biomass and the groups are linked through their trophic interactions. The Ecopath model is based on two fundamental equations: first, to describe the production term of the system, Eq. 1: Production = predation mortality + fishing mortality + biomass buildup + emi/immigration + other mortality; and second, that which satisfies the energy balance within each functional group: Eq. 2: Production = Consumption - Respiration - Unassimilated food.

Although the Ecopath model has the capability to include flows into or out of the system (Eq. 1), for the purposes of this model, no emi-/immigration, biomass build-up, nor fishing was considered. The first equation deals with balancing the production terms between groups for the model while the second equation ensures that each group is balanced within. The equations are linked through the common production term. For a system with n groups, n linear equations can be written and a series of simultaneous equations are set up for each group and solved using a generalized method for matrix inversion which is described by Mackay (1981). The routine solves for one of four parameters for each group, which are biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B) or ecotrophic efficiency (EE), a measure of how much of a group is used within the system.

The data for the Life-Support System Model

The ecosystem model was produced to represent the system in the 1980s. The dataset used for this study is a condensed version of a full model of the system (Gurney & Pakhomov, unpubl.). Biomass estimates for all biota and rate measurements (production and consumption), along with diet compositions and assimilation rates were made from the published literature of PEI and other sub-Antarctic systems. Trophic linkages were made from diet and stable isotope signatures. There are a total of 21 functional groups, divided into 15 consumers, four primary producers and two detrital groups. Where possible, data from the PEI were used, parameters were otherwise taken from ecosystem models of similar systems (Bradford-Grieve *et al.*, 2003; Cheung *et al.*, 2005; Pruvost *et al.*, 2005).

Biomass estimates

The mammalian and avian top predators are represented by five groups: the seals [southern elephant seal *Mirounga leonine* (Linnaeus 1758), sub-Antarctic fur seal *Arcto-*

cephalus tropicalis (Grey, 1872) and the Antarctic fur seal *Arctocephalus gazella* (Peters, 1875)], the penguins [kings, *Aptenodytes patagonicus* (Miller, 1778), macaroni *Eudyptes chrysolophus* (Brandt, 1837), southern rockhopper *Eudyptes chrysocome filholi* (Hutton, 1878) and gentoo *Pygoscelis papua* (Forster, 1781)], the albatross [wandering *Diomedea exulans* (Linnaeus, 1758), grey-headed *Thalassarche chrysostoma* (Forster, 1785), yellow-nosed *T. carteri* (Rothschild, 1903) and both light-mantled sooty *Phoebastria palpebrata* (Forster, 1785) and dark-mantled sooty *P. fusca* (Hisenberg, 1822)], the giant petrels (both northern *Macronectes halli* (Mathews, 1912) and southern *M. giganteus* (Gmelin, 1789)] and a group representing the majority of the small flying birds (petrels and prions) that breed at the islands (Appendix 1). Kelp gulls *Larus dominicanus* (Lichtenstein, 1823), Subantarctic skuas *Catharacta antarctica lonnbergi* (Lesson, 1831), the Crozet shag *Phalacrocorax melanogenis* (King, 1828) and the lesser sheathbill *Chionis minor marionensis* (Peters, 1934) were not included in the model. Population estimates are available for breeding populations of the top predators on the islands and biomass estimates were based on published estimates from the 1980s (Hanel and Chown, 1998). Adjustments in biomass estimates were made for all groups to account for the period of time that each group is considered resident at the islands (Condy, 1979; Cooper and Brown, 1990). Biomass estimates for mammalian groups include the full population, while for the avian fauna, only breeding populations are included.

The fish groups were divided into two demersal and two pelagic groups with the separation between large and small fish based on the maximum length attained by each species (small groups total length < 50 cm, large groups total length > 50 cm). Two families are considered the most important at the islands, the nototheniids and the myctophids. The demersal groups include benthopelagic and demersal species. The large demersal fish group consists of 21 species. This group includes three nototheniid fish, (the grey rockcod *Lepidonotothen squamifrons* (Günther, 1880), black rockcod *Notothenia coriiceps* (Richardson, 1844) and the marbled rockcod *Notothenia rossii* (Richardson, 1844)) all bathydemersal and benthopelagic species, as well as the sharks and rays. The small demersal fish group consists of 13 species and incorporates the inshore and continental slope fish species. Important species in this group include inshore nototheniid species, the lobe-lip notothen *Gobionotothen marionensis* (Günther, 1880) and *Gobionotothen acuta* (Günther, 1880), as well as the painted notie (*Lepidonotothen larseni* Lonnberg, 1905) which is also found on the continental slope. The large pelagic group contains 11 species and is dominated by the nototheniid Patagonian toothfish *Dissostichus eleginoides* (Smitt, 1898). The small pelagic fish are dominated by the Myctophidae family which comprise 17 of the 35 species. Myctophids are the most abundant pelagic

fish in the Southern Ocean (Gjosaeter and Kawaguchi, 1980; Sabourenkov, 1991; Kozlov, 1995) and are an important food source for many of the top predators (Adams and Klages, 1987; Brown *et al.*, 1990; Cherel *et al.*, 1993; Lea *et al.*, 2002).

Pelagic system biomass estimates for phytoplankton, zooplankton and pelagic fish groups were from the PEI, while biomass estimates for small pelagic fish group and the cephalopods were taken from general Southern Ocean estimates. The PEI system is notably different from many of the other sub-Antarctic islands, such that it lacks a large shelf area, like that of the Kerguelen archipelago. Macrozooplankton densities over the plateau at the Kerguelen Islands are higher (Hunt *et al.*, this vol.) and many of the top predator diets are dominated by zooplankton. While PEI do support locally high zooplankton biomass around the fringe of the islands, summaries of the diets of the most abundant predators indicate that myctophids are the most important prey species for the vertebrate predators found in the island system. Fish fauna studies carried out in the 1970s and 1980s (Gon and Klages, 1988), along with the recent 2001 survey (Pakhomov *et al.*, 2006), have provided a comprehensive list of species present at the island. Quantitative assessments, however, are still lacking. Biomass estimates for all fish groups were made using CPUE data from Brandao *et al.* (2002) and Pakhomov *et al.*, (2006). Similarly, species composition of cephalopods is known (largely from diet analysis of the top predators at the islands) but quantitative estimates on biomass are not known and estimates for the model were based on assessments from other sub-Antarctic systems.

The PEI have a rich benthic community; biomass estimates for the benthic components of the ecosystem were taken from the PEI data for all groups (Perissinotto and McQuaid, 1990; Attwood *et al.*, 1991; Beckley and Branch, 1992). Studies on the inter-tidal and benthic fauna of the islands were conducted in the 1980s providing a comprehensive list of species present, and a review of the ecology of the community (Blankley, 1984; Blankley and Branch, 1984; 1985; Blankley and Grindley, 1985; Arnaud and Branch, 1991; Branch *et al.*, 1991a; Branch *et al.*, 1991b; Beckley and Branch, 1992; Branch and Williams, 1993; Branch, 1994). The benthic community is approximately composed of 550 species with seven benthic community groups. *Nauticaris marionis* (Bate, 1888), the benthic decapod has the second highest crustacean biomass and numerous studies have focused on this benthic shrimp because of its perceived key role in the ecosystem (Perissinotto and McQuaid, 1990; Kuun *et al.*, 1999; Pakhomov *et al.*, 1999; Pakhomov *et al.*, 2000; Pakhomov *et al.*, 2004). The decapod is consumed by some of the top predators on the islands, notably the penguins (Brown *et al.*, 1990), and therefore provides a link between benthic autochthonous production and higher vertebrates. The benthic fauna are represented in this study by two

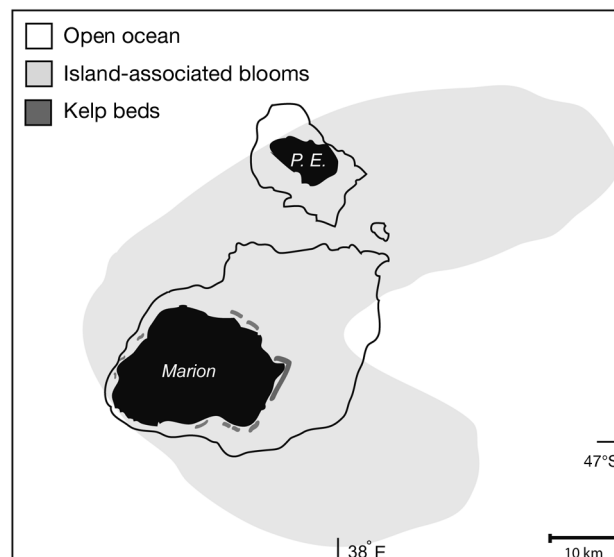


Figure 2. - Map of the Prince Edward Islands, indicating the spatial distribution of the three primary producers.

functional groups: one which represents the benthic fauna as a whole, the second one which represents the decapods.

An illustration of the spatial distribution of the three forms of primary production is shown in figure 2. The first comprehensive study of the phytoplankton and zooplankton of the area was conducted in the late 1970s (El-Sayed *et al.*, 1979a; El-Sayed *et al.*, 1979b; Grindley and Lane, 1979). Of all the pelagic groups in the system, the zooplankton has received the most attention. Studies describing the zooplankton fauna through the 1980s (Miller, 1985; Boden and Parker, 1986; Perissinotto and Boden, 1989) were followed by community assessments through the 1990s (Perissinotto, 1989; Perissinotto and Boden, 1989; Perissinotto and McQuaid, 1992b) and early 2000s (Hunt *et al.*, 2001; 2002; Bernard and Froneman, 2003; Hunt and Pakhomov, 2003). It has been found that the islands do not have an endemic zooplankton community; species of subtropical, sub-Antarctic and Antarctic origin have been found (Pakhomov and Froneman, 1999b), and the abundance and distribution of zooplankton groups varies at both temporal and spatial scales (Hunt *et al.*, 2001; 2002). For the purposes of this study, the zooplankton has been divided into three functional groups: the large crustaceans (dominated by euphausiid biomass), small herbivorous crustaceans (dominated by copepods) and all remaining zooplankton.

The open ocean phytoplankton was divided into two groups: the microphytoplankton, and the nano- and pico phytoplankton. *In situ* measurements of chl-a in the vicinity of the open ocean range from < 0.1 - 0.52 mg.m^{-3} (four studies: Froneman and Balarin, 1998; Froneman and Pakhomov, 2000; Bernard and Froneman, 2005; McQuaid and Froneman, 2008). Remotely-sensed ocean colour satellite data at

1 km resolution over a six by six degree area centred over the islands (44°S to 50°S, and 35°E to 41°E) from SeaWiFs (1998 to 2004) and a two by two degree area (45.8°S to 47.8°S and 36.8°E to 38.8°E) from MODIS (2005-2008) satellites show a total annual average value of 0.22 mg chl-a.m⁻³ using standard processing. This value was used in conjunction with a euphotic depth of 100 m (Cheung *et al.*, 2005), a chl-a to carbon ratio of 1:43.9 and a carbon to wet weight ratio of 1:9 (Christensen and Pauly, 1995). A total biomass for open ocean primary producers was estimated to be 8.69 t.km⁻². A summary of the contribution of microphytoplankton to the whole phytoplankton community was estimated at approximately 20% (El-Sayed *et al.*, 1979b; Froneman *et al.*, 1998; Read *et al.*, 2000). No explicit additional production associated with elevated productivity of the fronts was incorporated despite these features falling within the considered area.

The island-associated blooms are usually the result of increased production of diatoms (mainly the chain-forming *Chaetoceros radicans* Schütt, 1895) (Boden *et al.*, 1988), *Rhizosolenia curvata* (Zacharias, 1905) and *Dictyocha speculum* (Ehrenberg, 1837) (Perissinotto, 1992) or *Fragilariopsis* spp. (McQuaid and Froneman, 2008). *In situ* studies of chl-a from within the vicinity of the islands range from 0.01-2.8 mg chl-a.m⁻³ (8 studies: El-Sayed *et al.*, 1979a; Miller *et al.*, 1984; Allanson *et al.*, 1985; van Ballegooyen *et al.*, 1989; Perissinotto *et al.*, 1990b; Froneman *et al.*, 2000; Perissinotto *et al.*, 2000). The phytoplankton blooms are dominated by diatoms and chl-a concentrations exceed 1.5 mg.m⁻³ (measurements of up to 2.8 mg.m⁻³ have been made) (Boden, 1988; Duncombe Rae, 1989b). Under non-bloom conditions, chl-a concentrations range between 0.05 and 0.45 mg.m⁻³ with the composition dominated by nano- and/or picophytoplankton (Perissinotto *et al.*, 2000; Bernard and Froneman, 2002). Remotely sensed ocean colour satellite chl-a data at a 1 km resolution from a sub-area centred on the islands (46.5°S to 47.1°S and 37.5°E to 38.3°E) from 1998 to 2008 was processed (SeaWiFs data 1998-2004, MODIS data 2005-2008). Monthly averages during summer months ranged between 0.4 and 1.4 mg chl-a.m⁻³ showing clear seasonal blooms in the vicinity of the islands. The annual average productivity for the sub-area was 0.27 mg chl-a.m⁻³. An average annual increase of 0.05 mg chl-a.m⁻³ over and above the open ocean value of 0.22 was attributed to the elevated production associated with the islands. A conservative euphotic depth of 20 m for the blooms was assumed (Perissinotto *et al.*, 1990c).

Macrocystis laevis and *Durvillea antarctica* are the two macrophytes that dominate the system. Quantitative estimates of the macrophytes were made from both photographs and diving surveys in the 1980s, with estimates of 63 500 t for *M. laevis* (Attwood *et al.*, 1991) and 3 300 t for *D. antarctica* (Haxen and Grindley 1985). An extrapolation of these

estimates to include macrophyte beds around PEI based on the percentage of the perimeter of Marion to Prince Edward results in a total biomass of 87 495 t for the system (Attwood *et al.*, 1991).

Detritus estimates were made using the empirical equation of (Pauly *et al.*, 1993). Using a primary production estimate of 17.155 gC.m⁻².yr⁻¹ (lower estimate) (Pakhomov and Froneman, 1999b), the annual estimate of detritus resulting from the open ocean phytoplankton productivity was 3.184 g.m⁻² (equivalent to t.km⁻²). Using a conversion of carbon to wet weight of 1:9, detrital input was estimated at 28.7 t.km⁻².

Rate measurements

P/B data were taken from the published literature for the PEI where possible or otherwise from similar systems. Open ocean production was estimated to be between 94-442 mgC.m⁻².d⁻¹ (Boden, 1988; Balarin, 2000). Island associated production ranged from 84 to 3 000 mgC.m⁻².d⁻¹ (5 studies: El-Sayed *et al.*, 1979b; Allanson *et al.*, 1985; van Ballegooyen *et al.*, 1989; Perissinotto *et al.*, 1990b; Balarin, 2000), resulting in P/B ratios of 150 yr⁻¹ for open ocean production and 200 yr⁻¹ for island-associated blooms. Production rates for *M. laevis* were measured in both April and August and the mean productivity was 9.6 gC.m⁻².d⁻¹ which resulted in an estimated P/B of 5.22 yr⁻¹ (based on a biomass of 11.5 kg.m⁻²) for macrophytes (Attwood *et al.*, 1991).

Q/B data was estimated using empirical equations for all the top predators, based on energetic demands (Nagy *et al.*, 1999), using the body mass of each group (Trites and Pauly, 1998; Ryan and Bester, 2008) and calorific content of diets (Burger, 1981; Croxall, 1984; Abrams, 1985; Clarke, 1985; Doidge and Croxall, 1985; Brown and Klages, 1987; Tierney *et al.*, 2002), with an assumption that water content was 70% along with the specific diet for each group. Q/B data for fish were calculated using the empirical equation of Palomares and Pauly (1998), and from the literature for the benthic and zooplankton groups. Diet matrixes and assimilation efficiencies used in the calculations were estimated from the literature and are presented in tables I and II.

Nested models to assess primary production at different scales

Four models of different sizes were created. The areas for each model were calculated with four different radius lengths (200 nm, 100 nm, 50 nm, 20 nm), each of which was centered at the midpoint between the two islands that make up the Archipelago (46°46'S, 37°51'E). For each of the four models, the biomass per unit area (t.km⁻²) was scaled according to the size of each ecosystem, i.e., higher biomass per unit area with smaller model size for all top predators as they were assumed to fill the entire area of each model (see Tab. I). The estimates for all benthic components including demersal fish, the benthic decapods, benthos, interisland

Table I. - Input parameter estimates for the four Life-Support System Models (P/B, Production to biomass ratio; Q/B, Consumption to biomass ratio; U/Q, Unassimilated consumption). \square : Denotes constant biomass per unit area as marine in origin and constant for all models.

Model Size (radius length nm)	200	100	50	20	P/B	Q/B	U/Q
Model Size (km ²)	431014	107754	26938	4310			
Functional Group	B (t.km ²)				/yr	/yr	
Seals	0.0045	0.0180	0.0720	0.4500	0.09	14.25	0.10
Penguins	0.0213	0.0853	0.3412	2.1324	0.14	40.84	0.21
Albatross	0.0003	0.0012	0.0046	0.0290	0.02	41.34	0.20
Giant Petrels	0.00005	0.0002	0.0007	0.0045	0.07	57.26	0.20
Prions and Petrels	0.00033	0.0013	0.0053	0.0329	0.16	144.84	0.24
Large demersal fish	0.0154	0.0615	0.2459	1.5369	0.20	2.94	0.20
Small demersal fish	0.0130	0.0520	0.2080	1.3000	0.43	6.82	0.20
Large pelagic fish	0.09	0.09	0.09	0.09	0.16	1.92	0.20
Small pelagic fish	4	4	4	4	1.16	9.54	0.20
Cephalopods	0.11	0.11	0.11	0.11	3.44	13.94	0.20
Benthos	0.5	2	8	50	2.50	10.00	0.20
Benthic decapod	0.038	0.152	0.608	3.8	1.45	4.42	0.20
Large zooplankton crustaceans	6	6	6	6	5	14.00	0.20
Small zooplankton crustaceans	15	15	15	15	10	43.00	0.20
All other zooplankton	7	7	7	7	24	96.00	0.20
Open ocean large phytoplankton	1.69	1.69	1.69	1.69	150		
Open ocean small phytoplankton	7	7	7	7	150		
Island associated blooms	0.00405	0.0162	0.0648	0.405	200		
Macrophytes	0.203	0.812	3.248	20.3	5.22		
Macrophyte Detritus	0.037139	0.148556	0.594224	3.7139			
Detritus	28.66	28.66	28.66	28.66			

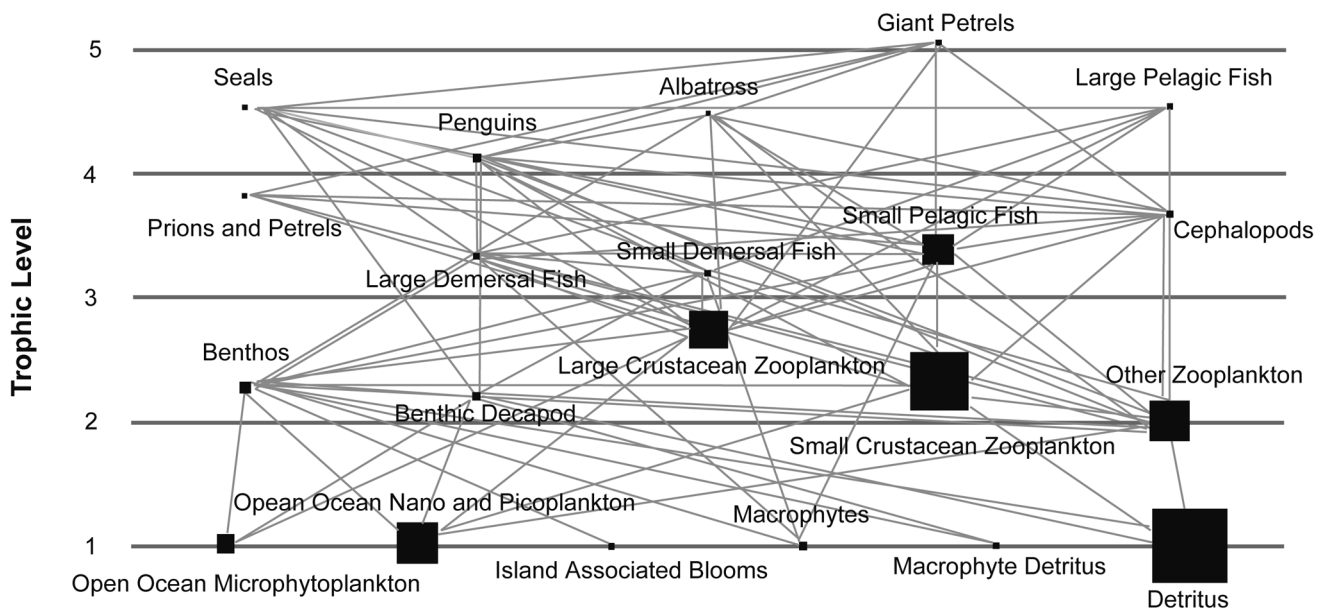


Figure 3. - Flow diagram with relative importance of each primary producer at 20 nm scale. Box size is proportional to the square root of the biomass of the functional group.

blooms and the macrophyte biomass, were scaled according to the area that their habitat occupied of the total area for each model i.e., higher biomass per unit area for each small-

er model. Pelagic system biomass estimates were assumed to be uniformly distributed throughout the areas considered and therefore the biomass per unit area for all pelagic groups

Table II. - Diet Matrix for the four Life-Support System models.

Group	Functional Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seals				0.06											
2	Penguins	0.00007	0	0.0023	0.781											
3	Albatross				0.00191											
4	Giant Petrels				0.001											
5	Prions and Petrels				0.02											
6	Large Demersals	0.0298	0.0003			0.001										
7	Small Demersals	0.0260	0.0007			0.005	0	0.004	0	0						
8	Large Pelagics	0.0859	0			0.001	0	0.0233	0	0						
9	Small Pelagics	0.6340	0.5528	0.4022	0.04	0.316	0	0.299	0	0	0.1773					
10	Cephalopods	0.2232	0.1058	0.5296	0.075	0.019	0	0.61	0	0	0.0591	0	0	0		
11	Benthos	0	0	0.0065		0.128	0.219	0	0	0.0088	0		0.1			
12	Benthic decapod	0.0006	0.0043	0		0	0.135	0	0	0	0	0.001	0.01			
13	Large zooplankton crustaceans	0.0006	0.1998	0.0302	0.022	0.095	0.1	0.063667	0.3585	0.3127	0.05	0.05	0.05	0.4	0.1	
14	Small zooplankton crustaceans	0	0.1281	0.0192	0.4	0.069	0.319	0	0.3584	0.3045	0.08	0.08	0.05	0.2	0.2	
15	All other zooplankton	0	0.0082	0.01	0.04	0.090	0.154	0	0.2713	0.1464	0.08	0.05	0.05	0.1	0.3	
16	Open ocean large phytoplankton	0	0			0	0	0	0	0	0	0.05	0.05	0.1	0.6	0.7
17	Open ocean small phytoplankton	0	0			0	0	0	0	0	0	0.05	0.05	0.3		
18	Island associated blooms	0	0			0	0	0	0	0	0	0.05	0.05			
19	Macrophytes	0	0			0.2764	0.0731	0	0.0031	0	0	0.02				
20	Macrophyte Detritus	0	0			0	0	0	0	0	0	0.1	0.37			
21	Detritus	0	0			0	0	0	0	0	0	0.519	0.37	1	0.1	0.3
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

remained unchanged for the each of the four models. Input data for all functional groups is presented in table I, and the diet matrix used for the model is presented in table II.

RESULTS

The trophic linkages for the purposes of this model have been based on the available data for the island system, and these relatively new trophic pathways have now been incorporated into this quantitative assessment which is illustrated in figure 3 at the scale of the EEZ. Only at this scale does the model balance, i.e., the energetic requirements for all the inhabitants are met. For the smaller size models, reductions in the land-based top predator biomass estimates are necessary for the models to balance. As none of these groups feed directly on the primary producers, the adjustments have no effect on how much of the production is directly used in the system and for the purposes of this study, will not be considered further. The relative biomass contributions of each of the producers at this scale are evident with the open ocean nano- and picoplankton contributing the most per unit area (Figs. 3, 4).

A quantitative assessment of the primary producers at the islands at each of the four scales considered, clearly shows the increased productivity per unit area with proximity to the islands demonstrating the basic principle of the 'island mass effect' (Fig. 4). The model constructed at the scale of the EEZ has a total producer biomass of 8.89 t.km⁻², while the smallest model has biomass contributions greater than three times this value at 29.395 t.km⁻². The open ocean production dominates in all but the smallest scale, where the macrophytes become important. Also evident from this assessment is the relatively small contribution the island associated blooms make to the system at all spatial scales. The greatest contribution of these blooms occurs in the smallest scale model, but even then contributes only 1.4% of the total primary producer biomass. If the assumption of the depth of the bloom be increased from 20 m to 120 m (Perissinotto *et al.*, 1990c), this contribution would have a maximum contribution of 7.5% at the smallest scale considered here.

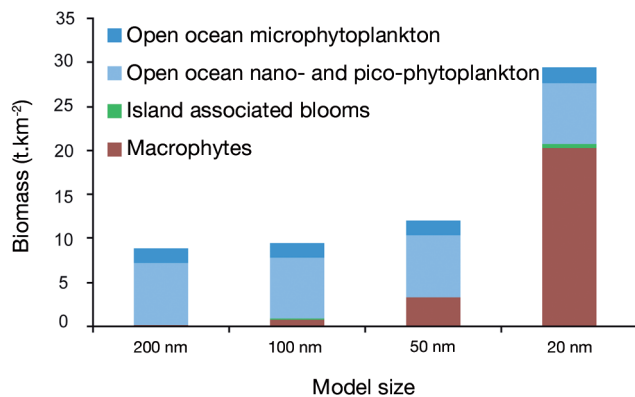


Figure 4. - Relative biomass of each primary producer for the four model sizes (Model sizes equivalent to circles with given radii).

These data provide an assessment of the biomass of the producers, but how much of this production is consumed within the system? The Ecopath routine, when provided with biomass, production and consumption rates, produces an Ecotrophic Efficiency (EE), given as a fraction of 1, which is a measure of how much of each group is used within the system (Fig. 5).

Of the two size fractions of open ocean phytoplankton production, the larger microphytoplankton portion is utilized the least. Ecotrophic Efficiency for this group increased with decreasing model size, but all EEs are relatively low (maximum EE at the smallest model size of 0.14). The smaller open ocean phytoplankton size fraction (the nano and picoplankton) has consistently high EE (between 0.84 and 0.87) suggesting that this source is well utilized in the system at all spatial scales.

As discussed, the contribution of the island-associated blooms to the total production is low. However, of this production, approximately 30% is consumed within the system. This EE is consistent because the consumers of this produc-

tion are the benthic fauna which are scaled with the model size, as are the blooms. This form of production is thought to enter the benthic sub-system through fallout following the blooms. Such a detrital component has not been explicitly separated in this model, the inclusion of which would add to the relative importance of this input.

At the smallest scale, while the macrophytes contribute approximately 69.1% of the available primary producer biomass, much of the production is not directly consumed as shown by the relatively low EEs (range 0.11-0.22). Even at the largest scale, relatively little of the macrophyte production is grazed on directly. Macrophyte detritus on the other hand is well used in the system: minimum EE of 0.60 in the smallest model and a maximum of 0.68 for the largest. This pattern is due to the diet of some of the pelagic components of the community consuming this form of detritus. The general detritus group follows the opposite trend with increasing EE with decreasing model size (0.35 to 0.63) largely attributed to the benthic fauna which directly consumes the macrophyte detritus.

DISCUSSION

Although the 'island mass effect' was recognised early on as a driving force behind enhanced local production at the PEI the mode of operation and subsequent transfer of primary production up the PEI food web continued to be a subject of research and source of contention for a number of years. Since the earliest investigations at the PEI, the open ocean allochthonous production was found to be low (average approximately $0.2 \text{ mg chl-a.m}^{-3}$) and studies were initially focussed on the autochthonous production, i.e., that of the island-associated blooms and the macrophyte production. During bloom conditions, chl-a concentrations were 5 to 10 times higher than average (between 1 and $2 \text{ mg mg chl-a.m}^{-3}$)

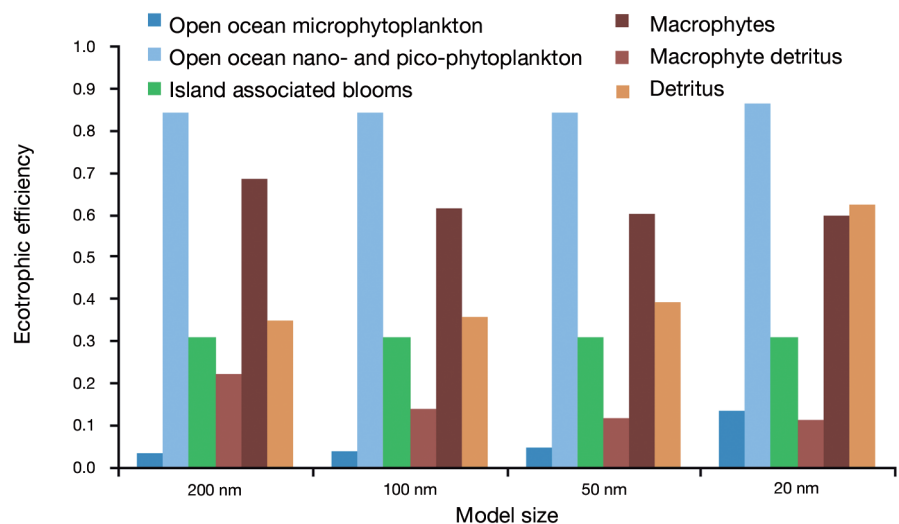


Figure 5. - Ecotrophic efficiencies for functional groups of the first trophic level of the four 'Life-Support System' models.

and this enhanced productivity was the result of seasonal blooms of diatom species (El-Sayed *et al.*, 1979b; Boden, 1988; Perissinotto *et al.*, 2000). Studies through the 1990s that focussed on zooplankton grazing showed no evidence of feeding on this microphytoplankton size fraction ($> 20 \mu\text{m}$) which dominates during such blooms, but grazing occurred in the nano- and pico- size fractions ($< 20 \mu\text{m}$) (Perissinotto *et al.*, 1990a). From these results, it appeared that the zooplankton community was adapted to consume smaller size fraction, available year round, and likely did not make use of the seasonal blooms. Production from the blooms was therefore thought to fall out of the surface waters and provide a direct transfer of primary production to the rich benthic subsystem with the pelagic community not directly benefiting from this form of production. A quantitative assessment of the macrophyte production in the vicinity of the islands was made in the 1980s and found to be greater per unit area than that of the local phytoplankton production, as was to be expected (Mann, 1973). However, this production was thought to contribute less to the seas around PEI because of its limited spatial coverage and because it was suspected that almost all of the macrophyte production was exported to the open ocean pelagic environment (Attwood *et al.*, 1991).

At this point, the two forms of autochthonous production were thought to have different fates: the blooms providing input into the benthic community and the macrophyte production being exported from the system. The issue of scale was not directly addressed in these assessments, but publications at the time estimated the ecosystem to be delineated by a 300 km radius, thought to be the extent of the foraging distance of the islands top predators (Adams *et al.*, 1993).

In the early 2000s, stable isotope studies conducted at the islands provided new insight into the trophic pathways in the PEI system. Unique carbon isotope signatures ($\delta^{13}\text{C}$) for each the three forms of production at the islands were identified (Kaehler *et al.*, 2000) and allowed for an assessment of the relative importance of each of the producers to the system. Input from macrophyte production, primarily as particulate carbon, to the near shore benthic community in particular, was shown to be substantial (Kaehler *et al.*, 2006), contradictory to earlier perceptions. From this, diet studies conducted in conjunction with stable isotope analysis (e.g., euphausiids (Gurney *et al.*, 2001), decapod *Nauticaris marionis* (Pakhomov *et al.*, 2004) and the fish community (Bushula *et al.*, 2005; Pakhomov *et al.*, 2006)) contributed to a better understanding of the trophic pathways for many of the key consumers. Two co-occurring near-shore fish species for instance, were found to have contrasting sources of production, one allochthonous and one autochthonous macrophytes (Bushula *et al.*, 2005). These data provided new insights incorporated into the LSS model, which allowed for the reassessment of the island system.

The relative importance of each of the producers is affected by the scale at which the system is assessed, a consideration seldom included in previous discussions on the PEI system. In all but the smallest spatial scale (where it contributes 23.8% to total available production), the small fraction (nano- and pico-) of the open ocean production dominates in terms of biomass per unit area (between 78.7% and 58.3% of total available production). This allochthonous production is the most important of the three sources at the PEI and may be considered the driving force of the island ecosystem, particularly at the larger spatial scales. When the producers are assessed in terms of what is actually consumed at the islands (the biomass combined with the EE outputs from the Ecopath routine), this component contributes in excess of 92.0% of the production at all but the smallest scale, where it contributes 69.5%. When all first trophic level contributors are included in the assessment (i.e., the two detrital groups along with the primary producers), the general detrital group dominates and the contribution of the allochthonous small size fraction of the open ocean production is reduced to between 32 and 37% for the three larger models, and 21% of the smallest model.

Of the two autochthonous contributors, the macrophytes were found to contribute the most to the ecosystem. When the total biomass of the producers in the system was assessed, the macrophytes contributed, in decreasing order of model size, 2.3%, 8.5%, 27.1% and 69.1%. Direct consumption of the macrophytes however was limited, therefore even at the smallest scale considered, when the available macrophyte biomass dominated the system, the amount consumed directly was 26.4% of the total producers consumed. Detritus generated from this production was well utilized in the system at all spatial scales (EE between 0.60 and 0.68); however, in terms of its contribution to the system when all first trophic level contributors are assessed (all producers and detrital groups), it is greatest at the smallest spatial scale at 7.70% of the total, which is similar to the contribution of the macrophytes themselves at 7.98%. The combined consumption of these two groups is substantial (15.68%), though it ranks third in terms of what is used in the system behind the general detrital component (62.10%) and the small open ocean contribution (20.99%).

The absolute biomass of the island-associated blooms is small compared to all other contributors, even at the smallest scale (less than 2% for all models). Approximately 30% of this production was consistently consumed within the system and its contribution, particularly in its detrital form, could be important to the benthic community. Inclusion of this component through an explicit contribution of its detrital form may provide further insight into the fate of this production, but from this assessment it appears to be limited.

A weakness of this assessment is the omission of the microbial loop. Microbial studies on microheterotrophs in

the PEI system have been conducted (Froneman and Balarin, 1998; Froneman and Bernard, 2004) and grazing impact of protists on phytoplankton may be between 47 and 71% of potential primary production per day (Froneman and Balarin, 1998). Bradford-Grieve *et al.* (2003) produced an ecosystem model of a sub-Antarctic system (Southern Plateau, NZ) which paid close attention to the microbial loop with five functional groups of the 19 considered dedicated to this section of the food web. No account was made in their assessment of the macrophyte production though its input particularly through the detritus was acknowledged (Bradford-Grieve *et al.*, 2003). Inclusion of this important component of the food web will further redefine models of the system.

CONCLUSION

For the time period considered in this study (the 1980s), allochthonous production, in the form of nano- and picophytoplankton, should be considered the most important contributor to the PEI system, and the driver of the island food web at all but the smallest spatial scale. This production reaches the top predators of the PEI ecosystem via zooplankton and small pelagic fish. Elevated phytoplankton productivity associated with the 'island mass effect' at PEI was found to be of little importance, even at the smallest scale considered here. The alternate form of autochthonous production, the macrophyte production was found to be utilized by both direct consumption and in its detrital form, and provides an important contribution to the system particularly when considered at the smallest scale. The benthic fish populations and near-shore top predators (e.g., gentoo penguins) are dependent on this autochthonous production, benthic-pelagic coupling (macrophyte production, benthic decapods and small demersal fish) thus represents an important trophic pathway in the system. Studies on the PEI ecosystem in the past decade have highlighted the importance of the autochthonous macrophyte contribution to the islands system. Indeed, we believe that this autochthonous component contributes towards a unique benthic habitat between the islands which warrants further detailed investigation. Overall, however, the findings of this study confirm previous perceptions that the system is largely reliant on pelagic allochthonous production. It was only at the scale of the PEI EEZ that the energy demands of the current population of PEI top predators were supported.

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Appendix 1. - Description of functional groups for the Prince Edward Islands Life Support System Models.

#	Functional Group	Species list	Species name	no. of spp.
1	Seals	Southern Elephant Seal Antarctic Fur Seal Subantarctic Fur Seal	<i>Mirounga leonina</i> <i>Arctocephalus gazella</i> <i>Arctocephalus tropicalis</i>	3
2	Penguins	King Penguin Macaroni Penguin Southern Rockhopper Penguin Gentoo Penguin	<i>Aptenodytes patagonicus</i> <i>Eudyptes chrysolophus</i> <i>Eudyptes chrysocome filholi</i> <i>Pygoscelis papua</i>	4
3	Albatross	Wandering Albatross Grey-headed Albatross Yellow-nosed Albatross Light-mantled Sooty Albatross Dark-mantled Sooty Albatross	<i>Diomedea exulans</i> <i>Thalassarche chrysostoma</i> <i>Thalassarche carteri</i> <i>Phoebetria palpebrata</i> <i>Phoebetria fusca</i>	5
4	Giant Petrels	Southern Giant Petrel Northern Giant Petrel	<i>Macronectes giganteus</i> <i>Macronectes halli</i>	2
5	Prions and Petrels	Fairy Prion Salvin's Prion Blue Petrel Great-winged Petrel Soft-plumaged Petrel Kerguelen Petrel Grey Petrel White-chinned Petrel Grey-backed Storm Petrel Black-bellied Storm Petrel South Georgian Diving Petrel Common Diving Petrel	<i>Pachyptila turtur</i> <i>Pachyptila salvini</i> <i>Halobaena caerulea</i> <i>Pterodroma macroptera</i> <i>Pterodroma mollis</i> <i>Lugensa brevirostris</i> <i>Procellaria cinerea</i> <i>Procellaria aequinoctialis</i> <i>Garrodia nereis</i> <i>Fregetta tropica</i> <i>Pelecanoides georgicus</i> <i>Pelecanoides urinatrix</i>	12
6	Large Demersal Fish	Blue antimora Southern seadevil Unicorn icefish Grenadier or rattail Slender codling Abyssal halosaur Mordid cod Grey rockcod Ridge scaled rattail Bigeye grenadier Finless flounder Black rockcod Marbled rockcod Longnose tapirfish	<i>Antimora rostrata</i> <i>Ceratias tentaculatus</i> <i>Channichthys rhinoceros</i> <i>Coryphaenoides</i> sp. <i>Halargyreus johnsonii</i> <i>Halosaurus macrochir</i> <i>Lepidion</i> sp. <i>Lepidonotothen squamifrons</i> <i>Macrourus carinatus</i> <i>Macrourus holotrachys</i> <i>Neoschiropsetta milfordi</i> <i>Notothenia coriiceps</i> <i>Notothenia rossii</i> <i>Polyacanthonotus challengerii</i>	15
7	Small Demersal Fish	Slickhead Messmate Triangular rockcod Lobe-lip notothen Austral cod South Georgia spiny plunderfish Painted notie Snailfish Antarctic armless flounder Marbled moray cod	<i>Alepocephalus</i> sp. <i>Echiodon cryomargarites</i> <i>Gobionotothen acuta</i> <i>Gobionotothen marionensis</i> <i>Guttigadus kongi</i> <i>Harpagifer georgianus</i> <i>Lepidonotothen larseni</i> <i>Liparididae</i> gen. sp. <i>Mancopsetta maculata maculata</i> <i>Muraenolepis marmorata</i>	13

#	Functional Group	Species list	Species name	no. of spp.
		Patagonian moray cod Cod & Haddock Southern flounder Antarctic horsefish	<i>Muraenolepis orangiensis</i> <i>Physiculus</i> sp. <i>Pseudomancopsetta andriashevi</i> <i>Zanclorhynchus spinifer</i>	
8	Large Pelagic Fish	Short snouted lancetfish Daggertooth Skate Patagonian toothfish Southern lanternshark Black dragonfish Porbeagle Barracudinas Southern barracudina Barracudinas Slender escolar Southern driftfish Skate/ray Bigthorn skate Smallscale waryfish Greenland shark Barracudinas	<i>Alepisaurus brevirostris</i> <i>Anotopterus pharao</i> <i>Bathyraja</i> sp. (tuff) <i>Dissostichus eleginoides</i> <i>Etmopterus granulosus</i> <i>Idiacanthus atlanticus</i> <i>Lamna nasus</i> <i>Macroparalepis</i> sp. <i>Magnisudis prionosa</i> <i>Notolepis</i> sp. <i>Paradiplospinus gracilis</i> <i>Psedoicichthys australis</i> <i>Raja</i> sp. <i>Rajella barnardi</i> <i>Scopelosaurus hamiltoni</i> <i>Somniosus microcephalus</i> <i>Stemonosudis</i> sp.	17
9	Small Pelagic Fish	Boulenger's snaggletooth Deep-sea smelt Pearleyes Snaggletooth Sloane's viperfish Smallhead flyingfish Black swallower Bristlemouth Lanternfish Rebains' portholefish Snaketooth Electron subantarctic Rough lanternfish Lanternfish Lanternfish Lanternfish False-midas lanternfish Nichol's lanternfish Lanternfish Southern blacktip lanternfish Lanternfish Diamondcheek lanternfish Stoplight loosejaw Lantern fish Magellanic rockcod Silver lightfish Tubeshoulder Crested bigscale Lanternfish Lanternfish	<i>Astronesthes boulengeri</i> <i>Bathylagus tenuis</i> <i>Benthalbella macropinna</i> <i>Borostomias antarcticus</i> <i>Chauliodus sloani</i> <i>Cheilopogon pinnatibarbus altipennis</i> <i>Chiasmodon niger</i> <i>Cyclothone</i> sp. <i>Diaphus</i> sp. <i>Diplophos rebainsi</i> <i>Dysalotus alcocki</i> <i>Electrona carlsbergi</i> <i>Electrona subaspera</i> <i>Gymnoscopelus bolini</i> <i>Gymnoscopelus braueri</i> <i>Gymnoscopelus fraseri</i> <i>Gymnoscopelus hintonoides</i> <i>Gymnoscopelus nicholsi</i> <i>Gymnoscopelus opisthopterus</i> <i>Gymnoscopelus piabilis</i> <i>Krefflichthys anderssoni</i> <i>Lampanyctus intricarius</i> <i>Malacosteus niger</i> <i>Nannobranchium achirus</i> <i>Paranotothenia magellanica</i> <i>Phosichthys argenteus</i> <i>Platytrichtidae</i> gen. sp. <i>Poromitra crassiceps</i> <i>Protomyctophum bolini</i> <i>Protomyctophum choriodon</i>	35

#	Functional Group	Species list	Species name	no. of spp.
		Norman's lanternfish Lanternfish Boa dragonfish Threelight dragonfish Slender lightfish	<i>Protomyctophum normani</i> <i>Protomyctophum tenisoni</i> <i>Stomias boa boa</i> <i>Trigonolampa miriceps</i> <i>Vinciguerria attenuata</i>	
10	Cephalopods	Cephalopods		>36
11	Benthos	Arthropods Brachiopods Molluscs Pycnogonids Echinodermata Annelids Coelenterata Bryozoa	Cirripedia Amphipoda Isopoda Tanaidacea Decapoda Reptantia Brachiopoda Solenogastres Bivalvia Gastropoda Polyplacophora Scaphopoda Cephalopoda Pycnogonida Asteroidea Ophiuroidea Echinoidea Holothuroidea Crinoidea Polychaeta Hydrozoa Bryozoa	1 68 32 12 4 8 3 1 35 53 3 1 1 17 33 22 2 10 2 89 11 19
12	Benthic decapod	<i>Nauticar</i>	<i>Nauticar</i>	1
13	Large crustacean zooplankton	Arthropods	Euphausiids Amphipods Decapods	14 18 6
14	Small crustacean zooplankton	Arthropods	Calanoid copepods Cyclopoid copepods Harpacticoid copepods Ostracods	48 4 2 6
15	Other zooplankton	Molluscs Annelids Ctenophores Cnidaria Chaetognaths Salps Appendicularians	Pteropods Cephalopods Polychaeta Ctenophores Hydrozoa Schyphozoa <i>Eukrohnia hamata</i> & <i>Sagitta</i> spp. <i>Oikopleura</i> spp. & <i>Frittilaria</i> spp.	8 8 9 2 10 1 2 3 2
16	Open ocean large phytoplankton	> 20 um in size, predominantly diatoms		
17	Open ocean small phytoplankton	< 20 um in size, nano- & picophytoplankton		
18	Island-associated blooms	Diatoms		
19	Macrophytes	Predominantly <i>Macrocystis laevis</i>		
20	Macrophyte detritus			n/a
21	Detritus			n/a